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ALEC B. COSTIN,[1] RU D. HOOGLAND,[2] AND C. LENDON[3]

ABSTRACT

Fossil leaf remains in *ca.* 5700-year-old lake deposits in the glacial Lake Mamsin (Guam) on the Saruwaged Plateau of New Guinea are compared with the floras of present-day grass-heath and forest in the area. The fossil flora is dominated by a broadleaf podocarp of the type now occurring at least 500 m. below the elevation of the lake (3500 m.). Fires of native origin are the most likely cause of the replacement of the former forest by grass-heath around the lake, but subsequently there may have been a cold phase ending about 2600 years ago which depressed the potential upper limit of the podocarp forest.

INTRODUCTION

Lake Mamsin (Guam) (lat. 147° 9′ E, long. 6° 21½′ S), near the head of the Kwama (or Gwama) River, is the most conspicuous evidence of Quaternary glaciation on the Saruwaged Plateau (cf. Loeffler, 1971). This area (fig. 1) was investigated by the first two authors, as members of the Seventh Archbold Expedition to New Guinea in 1964. The lake itself (approx. elev. 3500 m.) appears to have been formed by cirque-excavation of relatively soft limestone behind a band of more resistant basalt on which moraine has been deposited. Following breaching of the moraine by the headwaters of the Kwama River, which flows from the southeastern end of the lake, the water level has been lowered by several meters. This lowering occurred in more than one stage as shown by the existence of raised shoreline features on the eastern side of the lake. Lake deposits are now found exposed above present water level. These deposits contain well-preserved plant remains which could throw light on the nature of earlier ecological conditions around the lake. The investigation of the plant remains is the subject of the present paper.

The vegetation surrounding the lake today consists of a grass-heath in which the most conspicuous species are listed in table 1. There is no forest upstream of the lake, although there are

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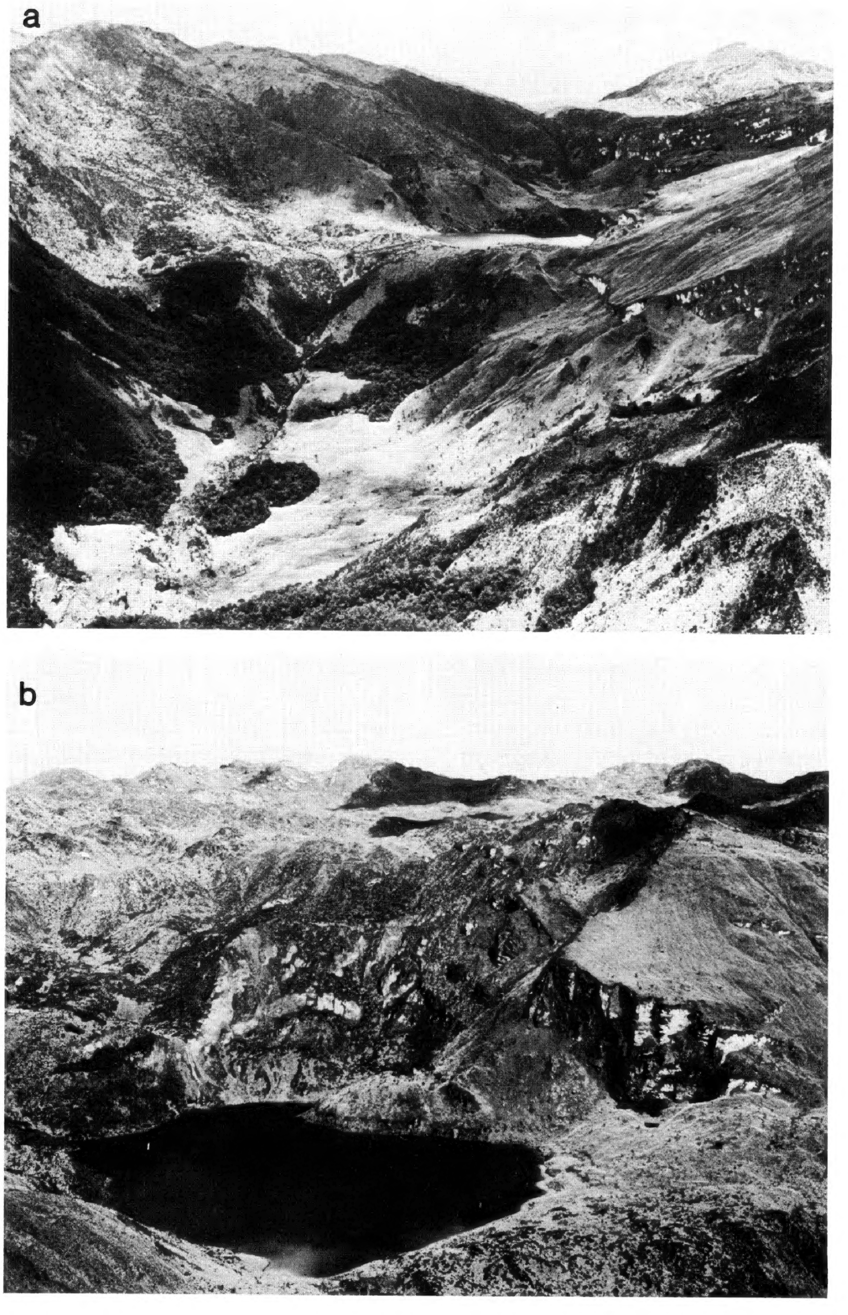


FIG. 1. a. General view of Lake Mamsin, showing the breached moraine on basalt. The vegetation surrounding the lake is a grass-heath. b. Closer view of Lake Mamsin, showing the moraine, raised shorelines and lake deposits. The lake deposits appear as the white edge along the water in the right foreground.

remnants of subalpine forest in the Kwama Valley not far below the lake, and at higher elevations elsewhere on the Saruwaged Plateau. The main species of the forest remnants are shown in table 2; it will be noted that broad-leaved podocarps are lacking. The latter apparently do not

occur in the Saruwaged area much above 3000 meters, some 500 meters in altitude below the level of the lake. The general distribution of forest and areas of botanical collection are shown on the map.

TABLE 1
Main Species in Present-day Grass-heaths surrounding Lake Mamsin

GRASSES
Danthonia archboldii Hitchc.
D. vestita Pilg.
Deschampsia klossii Ridl.
Deyeuxia arundinacea (L.) Jansen
D. brassii (Hitchc.) Jansen
Dichelachne rara (R. Br.) J. W. Vickery
Festuca crispato-pilosa N. L. Bor.
F. papuana Stapf.
Hierochloe redolens R. Br.
Monostachya oreoboloides (F. Muell.) Hitchc.
Poa crassicaulis Pilg.
P. minimiflora R. Br.
P. nivicola Ridl.
FERNS
Cyathea gleichenioides C. Chr.
C. muelleri Bak.
Gleichenia bolanica Ros.
G. erecta C. Chr.
G. hooglandii Holtt.
G. vulcanica Bl.
FORBS
Astelia papuana Skottsb. (Liliaceae)
Cotula leptoloba Mattf. (Compositae)
Epilobium keysseri Diels (Onagraceae)
Keysseria radicans (F. Muell.) Mattf. (Compositae)
Ranunculus saruwagedicus Hj. Eichl. (Ranunculaceae)
Senecio papuanus (Laut.) Belch. (Compositae)
S. sp. sp. nov.
Tetramolopium ciliatum Mattf. (Compositae)
T. macrum (F. Muell.) Mattf.
T. spathulatum Mattf.
SMALL SHRUBS
Coprosma divergens W. Oliv. (Rubiaceae)
Drapetes ericoides Hook. f. (Thymelaeaceae)
Gaultheria mundula F. Muell. (Ericaceae)
Haloragis halconensis Merr. (Haloragidaceae)
Hypericum saruwagedicum Diels (Hypericaceae)
Rhododendron commonae Foerst. (Ericaceae)
Styphelia suaveolens (Hook. f.) Warb. (Epacridaceae)
Trochocarpa dekockii (J. J. Sm.) H. J. Lam (Epacridaceae)

ACKNOWLEDGMENTS[1]

Valuable assistance was provided by the staff of the Herbarium Australiense, in the identification of fossil leaves, and by Dr. R. B. Knox, Botany Department, Australian National University, in freezing and sectioning of the leaves for microscopic examination. The carbon-14 dating of the fossil wood in the lake deposits and of the peats in Limestone Valley was carried out by Yale University Radiocarbon Laboratory. The map was prepared by Mr. M. L. White, CSIRO Division of Land Research, and the painstaking photography of the fossil leaves and thin sections, of which only a few of the photographs are reproduced herein, was by Mr. C. Totterdell, CSIRO Division of Plant Industry. The investigation was finalized while one of the authors (Cos-

TABLE 2
Main Species in Forest Vegetation below Lake Mamsin and in Forest Remnants of Saruwaged Plateau

Arrhenechthites novoguineensis (S. Moore) Mattf. (Compositae)
Dimorphanthera megacalyx Sleum. (Ericaceae)
Drimys piperita Hook. f. (Winteraceae)
Elaeocarpus polydactylus Schltr. (Elaeocarpaceae)
Eurya albiflora C. T. White and Francis (Theaceae)
E. tigang Laut. & K. Sch.
Olearia lepidota Mattf. (Compositae)
O. platyphylla Mattf.
O. rufa Koster
Papuacedrus papuana (F. Muell.) Li (Cupressaceae)
Pittosporum pullifolium Burk. (Pittosporaceae)
Prunus grisea (C. Muell.) Kalkm. (Rosaceae)
Quintinia sp. (Saxifragaceae)
Rapanea sp. (Myrisinaceae)
Rhododendron commonae Foerst. (Ericaceae)
R. culminicolum F. Muell.
R. pachycarpon Sleum.
R. saruwagedicum Foerst.
R. yelliottii Warb.
Schefflera sp. (Araliaceae)
Senecio sp. (Compositae)
Syzygium sp. (Myrtaceae)
Trochocarpa papuana (Wright) Sleum. (Epacridaceae)
Vaccinium amblyandrum F. Muell. (Ericaceae)
V. amplifolium F. Muell.
V. keysseri Diels
V. striicaule Sleum.

[1]Results of the Archbold Expeditions. No. 99.

tin) was working as Visiting Fellow in the Department of Biogeography and Geomorphology, Australian National University, Canberra.

MATERIALS AND METHODS

Approximately 2 meters of lake deposits are exposed above water level along the eastern shoreline. They extend for at least another 0.7 meter and probably for a considerably greater depth below water level. At approximately 200-230 cm. from the surface, there are well-preserved plant remains containing leaves, twigs, inflorescences, and fruits. Some plant remains also occur in smaller quantities at greater depths.

The field characteristics of the deposits are as follows:

0-15 cm. Black humus
15-50 cm. Pale yellowish limestone sand
50-60 cm. Dark-colored band of humic material, with flecks of limestone
60-90 cm. Yellowish clayey limestone sand
90-100 cm. Dark-colored band of humic material, with flecks of limestone
100-145 cm. Yellowish clayey limestone sand
145-150 cm. As above, but with humic band
150-175 cm. Yellowish limestone sand
175-200 cm. Yellowish limestone sand, with increasing amounts of organic matter and leaves
200-230 cm. Yellowish sandy limestone clay, containing abundant plant remains
230-250 cm. As above, but with fewer plant remains
250-270 cm. Greenish sandy clay, few plant remains

The deposits were sampled for future pollen analysis, and large samples of the 200-230 cm. leaf layer were collected for macroscopic examination and radiometric dating. A sample from 230-250 cm. was also obtained for dating.

The plant remains were washed out at the CSIRO laboratories in Canberra as carefully as possible from the surrounding limestone detritus, and stored in a preservative mixture of glycerine, alcohol, and formalin. An initial sorting was made of the plant remains into (a) "fruits," including buds, inflorescences and seeds; (b) leaves, and (c) wood, including pieces of stem and twig.

Wood samples from the 200-230 and 230-250 cm. layers were selected for carbon-14 dating, and the rest of the wood material was retained for anatomical examination. The remainder of the fruit and leaf material was carefully examined in the Herbarium Australiense in Canberra against reference material of New Guinea highland flora.

The first separation of the abundant leaf material was on the basis of size and shape. The resulting groups were then examined more critically under the binocular microscope and subdivided further on the basis of leaf venation, arrangement of the stomata, and characteristics of the cuticle. Matching against herbarium specimens was then carried out, to a generic and in some cases a specific level (figs. 2-3).

Where groups of leaves could not be matched exactly with herbarium specimens, the closest matching fossil and herbarium leaves were sectioned and examined microscopically. This proved to be critical for some leaves suspected of being podocarps, the transverse sections of which were examined for characteristic resin ducts. The uncertainty in distinguishing leaves of *Drimys* and *Prunus* on external appearance was also resolved by examining the cellular arrangement as shown in transverse section; in this instance the doubtful leaves were identified as *Drimys*, not *Prunus*, on the basis of the presence of oil glands. Some leaves, initially identified as *Rhododendron* on macroscopic characteristics, were also reassessed as *Rapanea* on the evidence of resin canals apparent in transverse section (fig. 4).

RESULTS

Most of the plant remains were in the form of leaves, of which about two-thirds consisted of identifiable fragments. The numbers and percentages of whole (or almost whole) leaves identified are shown in table 3. Note that only two of the fossil species, *Styphelia suaveolens* and *Trochocarpa dekockii*, are also listed in table 1 as main species at present growing in the grass-heaths near the lake.

The composite wood sample from the 200-230 cm. horizon from which the leaves and

wood were identified had a radiometric age of 5660 ± 80 years (Y – 1619). The wood sample from the 230-250 cm. horizon had an age of 6420 ± 80 years (Y – 1620).

Discussion. The present vegetation in the catchment of Lake Mamsin consists mainly of grassland and grass-heath, with limited occurrences of bog vegetation. At the highest levels (approx. 4000 m.) the grassland and grass-heath vegetation is climax, but much of it on the Pla-

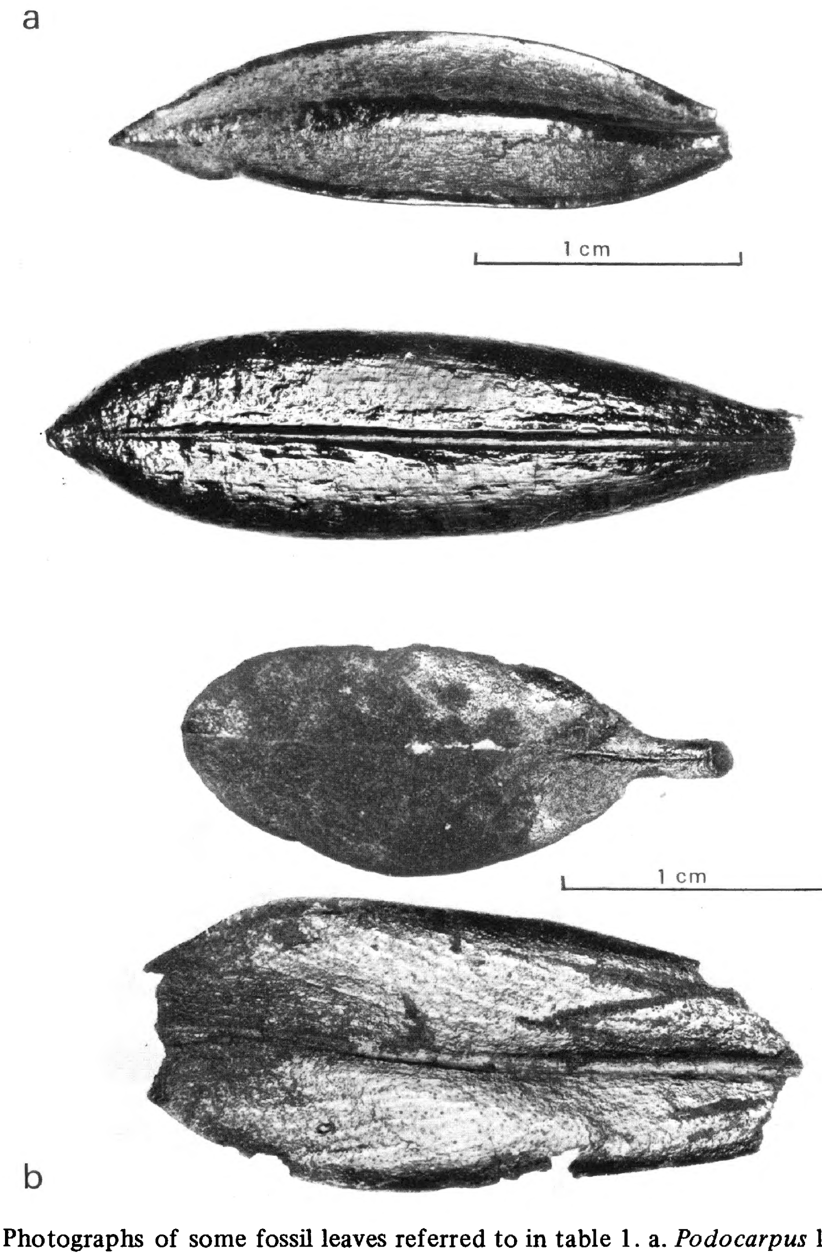


FIG. 2. Photographs of some fossil leaves referred to in table 1. a. *Podocarpus* leaves (×5). Note the broad, well-defined midrib, the thickened margins, and the lack of well-defined venation. b. *Rapanea* leaves (×5). Note the sunken appearance of the midrib.

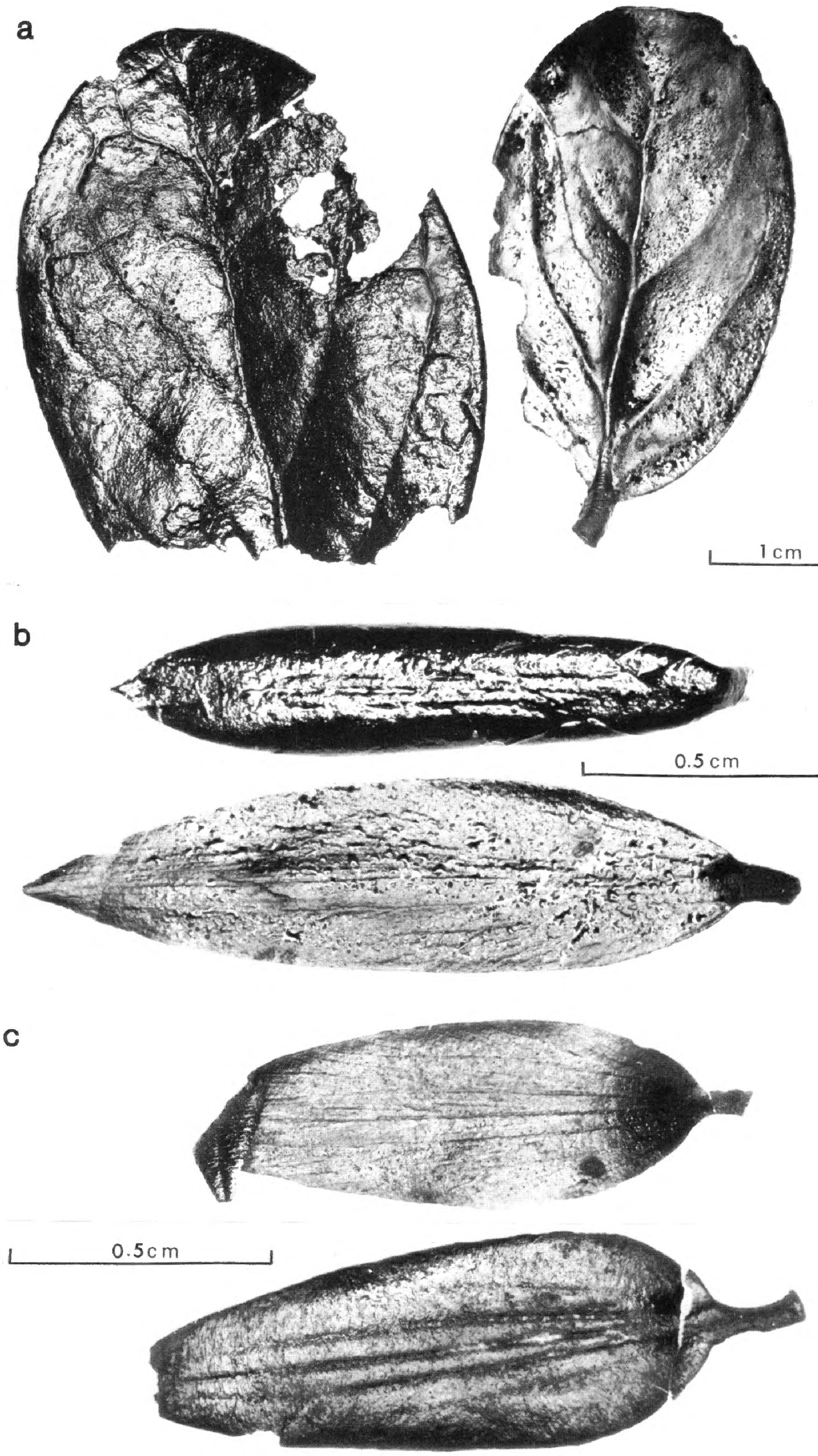


FIG. 3. Photographs of some fossil leaves referred to in table 1. a. *Vaccinium amplifolium* leaves (×3), showing characteristic venation. Pitting occurs on the undersurface. b. *Styphelia suaveolens* leaves (×10). c. *Trochocarpa dekockii* (×10), showing characteristic venation.

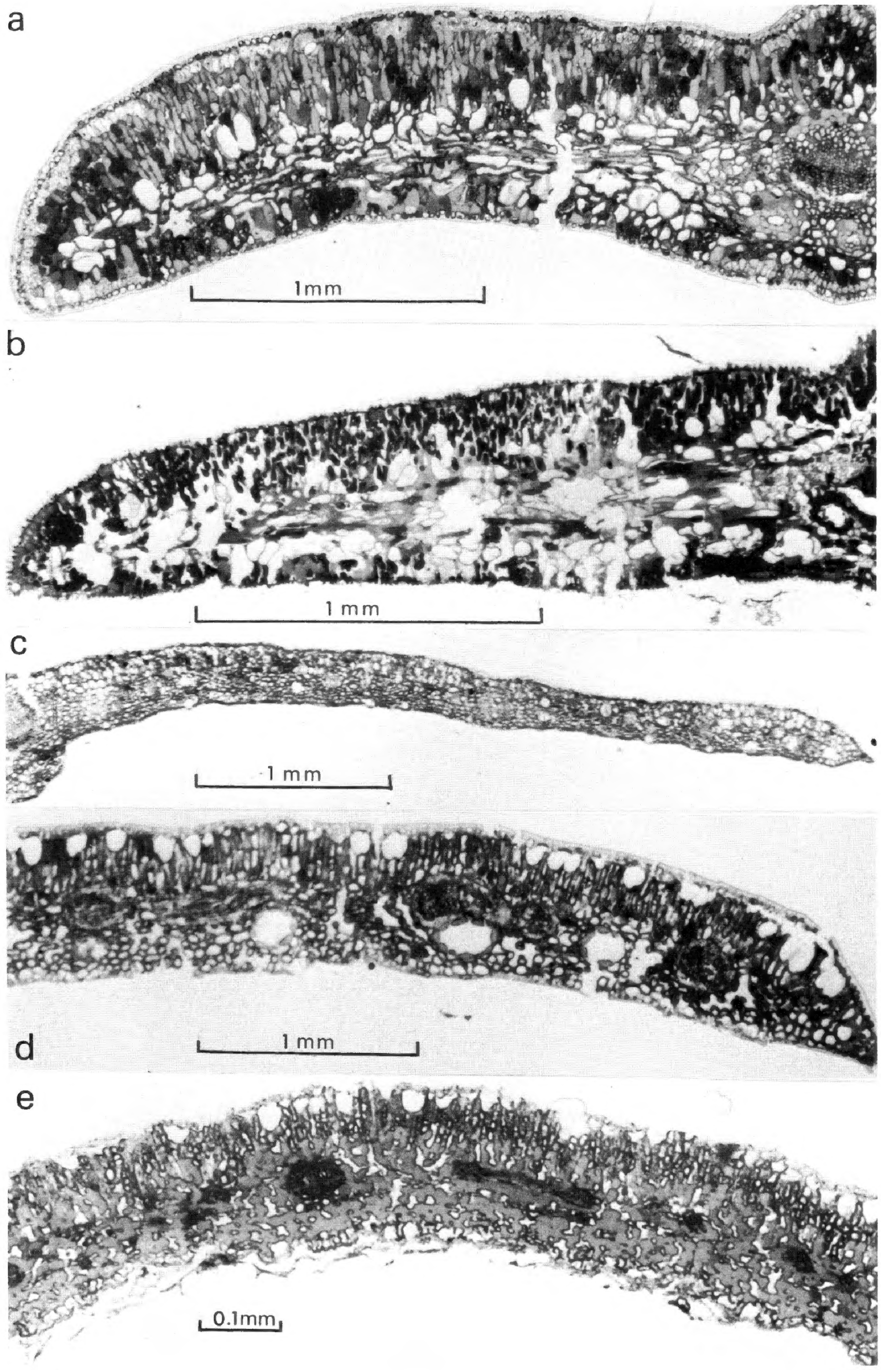
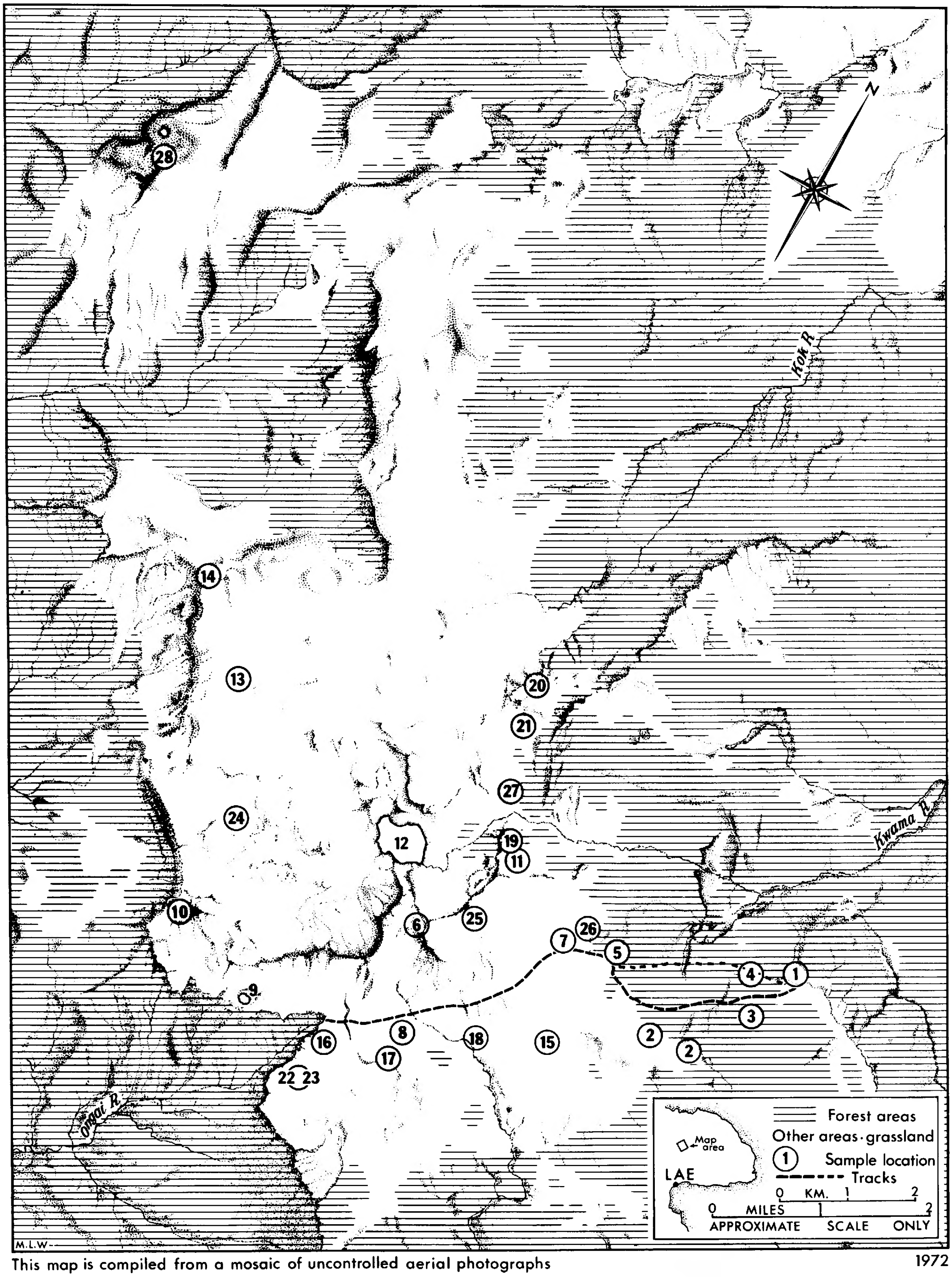


FIG. 4. Microphotographs of transverse sections of fossil leaves referred to in table 3, and of some herbarium leaves. a. Fossil leaf of *Podocarpus*, showing resin canals. b. Leaf of *Podocarpus brassii* from Herbarium Australiense, showing resin canals. c. Fossil leaf of *Drimys* showing oil glands which help distinguish leaves of this genus from morphologically similar leaves of *Prunus*. d. Fossil leaf of *Rapanea* showing oil glands which help to distinguish leaves of this genus from morphologically similar leaves of *Rhododendron*. e. Fossil leaf of *Rhododendron* (affin. *R. saruwagedicum*); there are no oil glands as in *Rapanea*.



MAP 1. Reconnaissance map of the Lake Mamsin (Guam) area, Saruwaged Plateau, showing general distribution of forests and treeless (mainly grassland) vegetation. The numbers (except 28) indicate botanical collecting sites: (12) refers to Lake Mamsin, (7) to Limestone Valley.

TABLE 3
Floristic Composition and Relative Abundance of Leaf Remains from Lake Mamsin

Group	No. of leaves	% of total count
Podocarpus	498	44
Epacridaceae	(554)	(50)
probably *Styphelia suaveolens*	300	27
probably *Trochocarpa dekockii*	254	23
Vaccinium amplifolium	35	3
Rapanea	23	2
Drimys and *Rhododendron*	4	<1
Cyathea macgregorii	Trace	Trace
Unidentified fern	Trace	Trace

teau generally and that surrounding the lake is undoubtedly disclimax, having replaced the original subalpine forest and scrub. As far as could be ascertained no substantial forest remnants occur within the catchment of the lake; although as has been noted (and see map) there are remnants elsewhere on the Saruwaged Plateau at elevations above and downstream from the lake. The species listed for these forest remnants (table 2) also include some found as fossils (table 3) but there is an absence of broad-leaved podocarps which dominate the fossil remains. Such podocarps apparently do not occur in the area within at least 500 meters below the elevation of the lake. Because of the excellent state of preservation of the 5660-year-old leaf remains, it is unlikely that they could have been transported far from the parent trees and shrubs. The lake deposits are therefore considered to reflect largely the composition of the local vegetation, rather than of vegetation of more distant parts of the catchment upstream. If this assumption is correct, it is possible to be more precise concerning the significance of vegetation changes around the lake within about the last 6000 years.

There are two feasible explanations for the change from broad-leaved podocarp forest to subalpine grassy heath; these explanations are not mutually exclusive. The simplest explanation is that fires of native origin have effectively deforested the area; this process, which has been going on in montane New Guinea for the last 5000 years (Walker, 1970), is still to be seen on other parts of the Saruwaged Plateau. The difficulty with this explanation alone is that Lake Mamsin is at least 500 meters above the present level of broad-leaved podocarps in the area; this suggests there has also been a climatic change since deforestation, toward slightly cooler conditions.

There is no difficulty in accepting native fires as the main cause of deforestation within the last 6000 years. Evidence to support the hypothesis for a lowering in temperature is less convincing. But there is some supporting evidence from the bog peats in Limestone Valley, approximately 3 km. east of the lake (see map). Here, accumulation of peat for more than 11,000 years (11,230 ± 100 years[1]; Y – 1622) has been interrupted by the deposition of limestone debris above which peat accumulation recommenced about 2600 years ago (2640 ± 80 years; Y – 1647). The inorganic deposition could have been caused by solifluction under slightly colder conditions than at present, as has been suggested for parts of highland Australia where there is evidence of a cold phase between about 3000 and 1500 years ago (Costin, 1973).

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[1]This is a significant date in itself, indicating the minimum period during which this part of the Saruwaged Plateau has been ice-free. It is in general agreement with the minimum ages of deglaciation of Mt. Wilhelm and the Carstensz mountains (Hope and Peterson, 1972).